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# Systematics of sun-squirrels (*Heliosciurus*) in eastern Africa

by

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Following Ingoldby's (1927) review of *Heliosciurus,* all sun squirrels then assigned to that genus were placed in *H. gambianus* (*Sciurus gambianus* Ogilby 1835, Gambia) by Ellerman (1940). But Rosevear (1963) showed that there were two sympatric species of *Heliosciurus* in West Africa, the smaller *H. gambianus* and the larger *H. rufobrachium* (*Sciurus rufobrachium* Waterhouse, 1842, Fernando Po), and he attempted to assign all named forms of sun squirrel, with the exception of *H. ruwenzorii,* to one or other of these species.

The oldest name for the larger forest sun squirrels of Zambia, Zimbabwe and Mozambique, north to southern Tanzania, is *Sciurus mutabilis* Peters, 1867 (Boror, Mozambique). Except in dimensions and the nail-like thumb claw, they show no particular resemblance to *H. rufobrachium,* to which Rosevear (1963) referred *mutabilis* as a subspecies. Some specimens are very similar in colour and colour pattern to *H. (gambianus) rhodesiae* of the miombo woodland (*Funisciurus annulatus rhodesiae* Wroughton, 1907, neighbourhood of Chiwale, Zambia). *H. rhodesiae* also has a nail-like thumb claw (Allen & Loveridge 1933) but is distinctly smaller with 95 percent of occipito-nasal skull length measurements ranging between 45.5 and 50.5 mm (n = 26, sample from Balovale), as against 52.5–57.8 mm for *H. mutabilis* (Table 1). *H. rhodesiae* and *H. mutabilis* are separated not only ecologically (Ansell 1978) but also geographically, by the Muchinga Scarp. No intermediates have been recorded. Nowhere is the range of *H. mutabilis* contiguous with that of *H. rufobrachium* (sensu Allen 1939). It is possible, therefore, to regard *H. mutabilis* as a separate species.

North of the Rufigi River in northern Tanzania and Kenya, *H. mutabilis* is replaced by *H. undulatus* (*Sciurus undulatus* True 1892, Mt Kilimanjaro). It is provisionally retained as a species distinct from *H. mutabilis* since there is no evidence yet for intergradation between them. *H. undulatus* also shows no evidence of intergradation with its very different neighbour to the north,

the isolate *H. keniae* (*Sciurus keniae* Neumann, 1902, Mt Kenya), assigned to *H. rufobrachium* by Rosevear (1963) but phenetically very much closer to specimens from Ethiopia he assigns to *H. gambianus* (see discussion in Kingdon, 1975: 421).

*H. mutabilis* and *H. undulatus* are hence separated geographically, morphologically and to a large extent ecologically from neighbouring populations of *Heliosciurus*. *H. rhodesiae,* though assigned to *H. gambianus* by Rosevear (1963), is possibly not immediately related to that species (Allen & Loveridge 1933) and probably intergrades with *H. rufobrachium* (Grubb, in prep.). Conceivably *H. mutabilis* and *H. undulatus* are related phylogenetically to *H. rufobrachium* through *H. rhodesiae,* but there appears to be no evidence for associating them preferentially with *H. rufobrachium* in the genus *Heliosciurus* at the moment.

Meester, Davis & Coetzee (1964) and Amtmann (1975) have synonymised some of the subspecific names of *H. mutabilis* and *H. undulatus,* and as these taxa can now be seen to be discretely segregated from other *Heliosciurus,* it is appropriate to analyse their geographic variation and assess the merits of these recent taxonomic decisions.

## Material

I have examined 118 skins and 75 adult or near-adult skulls of *H. mutabilis* and 38 skins and 27 adult or near adult skulls of *H. undulatus* in the British Museum, Natural History (BM), the American Museum of Natural History, New York (AMNH), the Field Museum, Chicago (FM), the Carnegie Museum, Pittsburg (CM), the National Museum of Natural History, Washington D. C. (USNM), the Zoological Museum, Humboldt University, Berlin (ZMB) and, as loan material, from the Transvaal Museum (TM).

## Pelage characters

*Heliosciurus mutabilis* and *H. undulatus,* like other members of their genus, have agouti-banded hairs. The number of bands varies from one part of the body to another as well as between populations. The body hairs usually have two light bands and three dark ones, including the base and the fine tip. The tail hairs have between three and 12 bands, always with a dark tip. Light bands are sometimes reduced in width or eliminated in more extremely melanised squirrels, and more rarely, the dark bands may be eliminated with extreme erythrism. The hair bands may or may not form discrete dark and light rings encircling the tail along its length. There is usually a clear demarcation between the denser dorsal pelage and the sparser ventral pelage, where the body hairs are shorter and do not usually have dark tips, but may have a single basal or subbasal dark band.

### *Heliosciurus mutabilis*

*H. mutabilis* is distinguished by the very striking colour changes in the pelage between moults, the holotype being an animal half way through moult, with both new and old fur (Peters 1852: Plate 30; Thomas 1892: 549). In fresh skins, the dark hair bands are blackish brown and the light ones deep ochre to whitish. As the pelage ages, the dark ground colour fades to maroon brown but the light bands are at first retained. As the moult commences, the hair bleaches still further to a light reddish ochre, with the light and dark bands now of similar tone and difficult to distinguish. Thomas (1894: 141) says that the hair bleaches "under the influence of the summer sun", but this effect, which is not seen in other *Heliosciurus* species, may be spontaneous. Specimens with bleached fur or with the moult just commencing on the snout are recorded from all months except July in the available sample, but specimens halfway through moult or with it almost completed are chiefly recorded from October to May, and those with fresh or relatively fresh fur, from April to December, as noted by Thomas (1892, 1894). There appears to be a single moult of the whole pelage as in the tropical Asian genus *Callosciurus* (Moore & Tate 1965: 201) rather than the double spring and autumn moult known from temperate zone squirrels.

When looking at geographic variation in *H. mutabilis*, then, only reasonably fresh skins can be compared. The populations from the eastern part of the species' range, from southeast Tanzania to southern Mozambique, are relatively pale, but with distinct orange sub-basal bands to the body hairs. They are referable to *beirae,* which is usually regarded as a synonym of *mutabilis.* Further inland, along the Zimbabwe border, they are replaced by deeper coloured more ochraceous animals, often with ochre belly, assignable to *chirindensis.* Smithers & Tello (1976) state this subspecies is known only from the type locality, in Zimbabwe but specimens from Tambarara, Mozambique, and some neighbouring localities can not be separated from topotypes of *chirindensis* except by their somewhat shorter tail hairs (though longer tail hairs are not a constant feature of *chirindensis* according to Roberts 1951) and they agree in having nine bands on these hairs.

In the Shire Highlands of southern Malawi, the squirrels are darker but less ochraceous and colder in tone, with the sub-basal body-hair bands paler and duller, and not infrequently with a broad black dorsal stripe. The type of *mutabilis* was described as having such a stripe (Peters 1852) and this is the name that should be accepted for these highland squirrels at the subspecific level (Thomas 1892: 549). The type locality of *mutabilis* is Boror (region?), a lowland area, but perhaps the type was not actually collected there. *Mutabilis* sensu stricto does occur however on Masindi Mt, some distance to the north, and possibly elsewhere in Mozambique. The species is still very poorly known from Mozambique north of the Zambezi, for which Smithers &

Tello (1976: 141) record it from only three quarter-degree squares. Roberts (1913) examined moulting specimens from Boror (town?) which do not appear to conform with the type, as they do not have the dorsal stripe. They agree more with *beirae* but being in moult they are difficult to assess. Roberts (1951) says that *mutabilis* is distinguished from *beirae* by having a smaller skull and white sub-basal bands to the body hairs, but in the original description of his specimens (Roberts 1913) he mentions orange buff sub-basal body hair-bands, while skull measurements based on additional material are not significantly different in the two forms (Table I). It is apparent that most specimens from Mozambique, perhaps even including Roberts' specimens from Boror, conform not to the type of *mutabilis* but to the type of *beirae,* while squirrels from the Shire Highlands and Masindi Mt do conform to *mutabilis*. Whatever the explanation of this situation, the name *mutabilis* should not be used in a subspecific sense for lowland squirrels, as has been done by a number of authors (Swynnerton & Hayman 1951, Ellermann, Morrison-Scott & Hayman 1953, Ansell 1960, 1964, Ansell & Ansell 1973, Kingdon 1974, Amtmann 1975, Smithers & Tello 1976). As references such as these have tended to use the name *'mutabilis'* in a broad sense to include what are here understood as *shirensis* and *beirae,* Meester, Davis & Coetzee (1964) acted quite reasonably in synonymising these names with *mutabilis*. They also thought that *smithersi* and *vumbae* were possible synonyms of *chirindensis*. This arrangement would imply a division into northern and southern subspecies, which is not in agreement with the conclusions presented here.

Squirrels from the Zimbabwe-Mozambique highlands (18° to 19°50'S, according to Smithers & Tello 1976) are like *mutabilis* but even darker, with the belly concolourous with the back. They are separated from *mutabilis* by about 300 km, and are referable to *vumbae*.

In Zambia, western Malawi, southeast Rhodesia and neighbouring parts of Mozambique, as well as in extreme south-west Tanzania, the lowland squirrels are paler again, not unlike *beirae,* but with a much less contrasting sub-basal body-hair band. The name for these squirrels is probably *shirensis,* as suggested by Allen & Loveridge (1933). The type locality of *shirensis* is the Shire River, running below the Zomba plateau. This name is based on three specimens (no lectotype has been selected) which are old, one bleached in life and the others rather faded, and now cannot be reliably separated from some faded *mutabilis* skins. Thomas (1892) indicated that *shirensis* only differed from *mutabilis* in lacking the dorsal black patch, and hence believed they were probably conspecific. They would now perhaps be regarded as synonymous, for only about half the available *mutabilis* specimens have the dark patch clearly developed, but the Shire River is at a lower altitude than the *mutabilis* localities, so the expectation is that the squirrel population

also has a lowland facies, never being as deeply pigmented as *mutabilis* sensu stricto. The type series indeed lack the woolly underfur characteristic of montane squirrels.

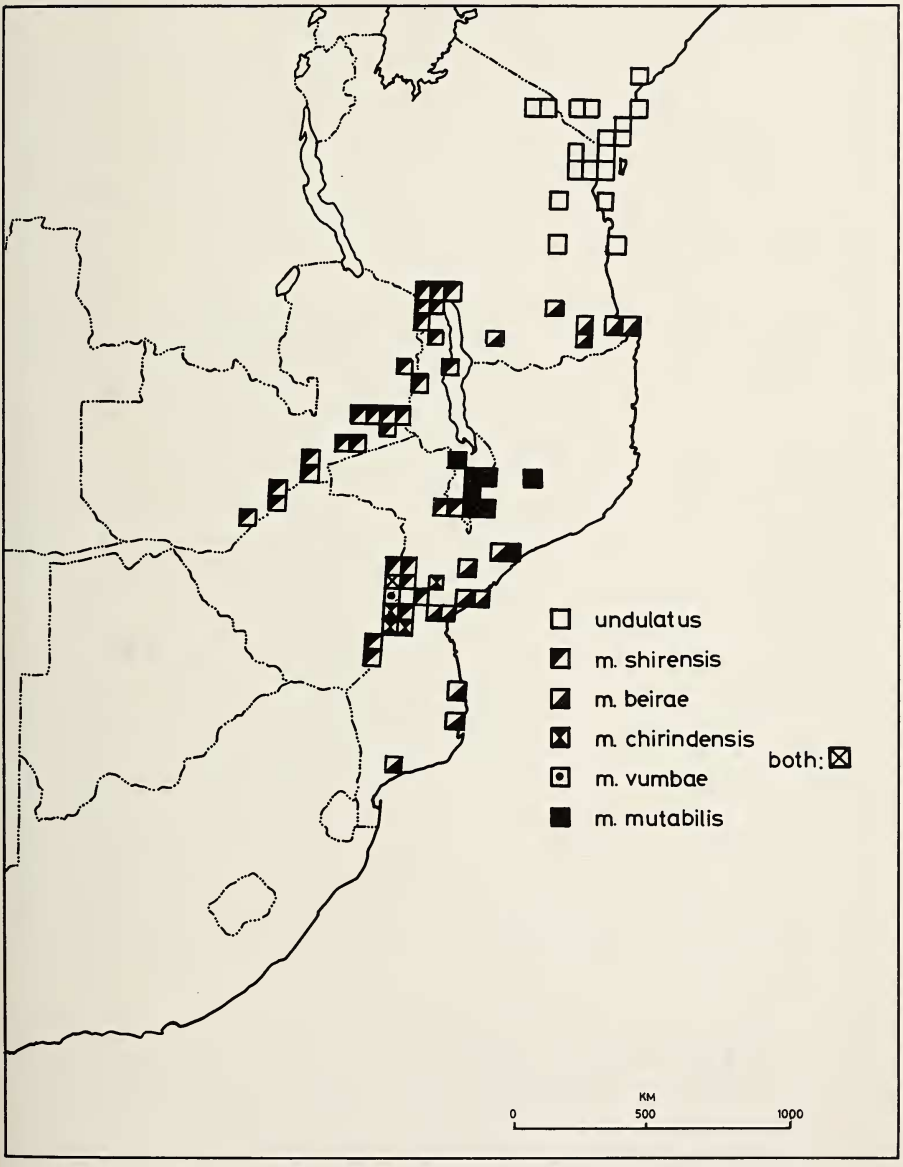


Fig. 1: Map of eastern Africa to show the distribution of *Heliosciurus mutabilis* and *H. undulatus*. Each symbol indicates occurrence within a half-degree square.

Some specimens of *shirensis,* as understood here, have the light hair bands almost white and Lundholm (1955) described one of these specimens from southeast Rhodesia as a new subspecies, *smithersi.* Smithers & Tello (1976) regard *smithersi* as the form occuring along the southern Zimbabwe-Mozambique border at relatively low altitudes, but squirrels of this same type are also recorded from the north-eastern montane area of Zambia (Ansell & Ansell 1973) and other scattered localities in Zambia. *Smithersi* is hence rather too polytopic to be regarded as a geographic race. In addition, the darker specimens of *shirensis* are hardly distinguishable from less heavily pigmented specimens of *mutabilis.* In this morphological continuum, it is not desirable to recognise three subspecies, even provisionally. I synonymise *smithersi* with *shirensis,* appreciating at the same time that typologically *smithersi* represents one extreme in the series.

Two specimens of *shirensis* from the Misuku range, northern Malawi, differ from all others in their long rather shaggy fur and in the exceptionally large number of bands on the tail hairs. They do not show any tendency towards melanism, as in the montane population from further south.

By attempting to match specimens from different localities, it is possible to state subjectively the phenetic relations between the subspecies recognised. *'Smithersi'* is the palest morph and comes nearest to *H. (gambianus?) rhodesiae* in colour. *Shirensis* grades into *mutabilis* which in turn grades into the darkest form, *vumbae,* although the two do not actually come in contact. It is not clear whether *vumbae* intergrades with *chirindensis* which may surround it. *Shirensis* also grades into the more ochraceous *chirindensis* which in turn grades into *beirae,* again a paler form and the one which geographically and in colour pattern comes nearest to *H. undulatus.* Over most of its range, then, *H. mutabilis* is a relatively pale-coloured lowland squirrel (subspecies *beirae* and *shirensis* ), but in isolated highlands in Mozambique, Malawi and Rhodesia, rather localised, deeply pigmented populations occur (*mutabilis, vumbae, chirindensis* ). Smithers & Tello (1976) recognised *smithersi* (i. e. *shirensis* ) and *vumbae* as separable from *chirindensis,* in agreement with my conclusions. They list *mutabilis* (i. e. *beirae* ), *smithersi* (i. e. *shirensis* ) and *vumbae* from Mozambique and remark that *chirindensis* may be expected to occur, which I confirm. *Mutabilis* sensu stricto also occurs, of course.

What I have said concerning the choice of subspecific names in *H. mutabilis* may smack of taxonomic juggling but is, I believe, justified. With uncertain type localities (*mutabilis* ), poor type material (*shirensis* ) and the need to conserve properly proposed and frequently utilised names, there appear to be few alternatives to the procedure I have adopted. The classification is nevertheless provisional, in the sense that it represents what I think is the best taxonomic assessment of available material, rather than of the natural

Table 1. Skull measurements of *Heliosciurus* species, in mm (mean ± standard deviation, sample size in parentheses)

| | Occipitonasal length | Condylobasal length | Zygomatic breadth |
|---|---|---|---|
| *H. mutabilis* | | | |
| ssp. *shirensis* | 54.9 ± 1.16 (11) | 50.4 ± 0.95 (11) | 32.4 ± 1.22 (11) |
| *mutabilis* | 55.1 ± 1.51 (15) | 50.4 ± 1.41 (20) | 31.8 ± 0.88 (20) |
| *vumbae* | 56.1 ( 2) | 51.7 ± 0.61 ( 3) | 32.4 ( 2) |
| *chirindensis* | 55.3 ± 1.58 ( 8) | 51.2 ± 0.79 ( 7) | 32.6 ± 0.74 ( 6) |
| *beirae* | 55.2 ± 0.82 ( 6) | 50.6 ± 1.12 ( 7) | 31.7 ± 1.02 ( 7) |
| all subspecies | 55.2 ± 1.31 (42) | 50.6 ± 1.19 (48) | 32.0 ± 0.99 (47) |
| *H. undulatus* | 53.9 ± 1.38 (16) | 49.9 ± 1.14 (17) | 31.6 ± 0.82 (18) |

Table 2. External measurements of *Heliosciurus* species, in mm (mean ± standard deviation, sample size in parentheses)

| | Head and body length | Tail length | Hind foot | Ear | Length of tail hairs |
|---|---|---|---|---|---|
| *H. mutabilis* | | | | | |
| ssp. *shirensis* | 250.0 ± 28.86 ( 9) | 274.1 ± 20.79 ( 9) | 56.4 ± 2.57 (11) | 18.1 ± 0.73 ( 9) | 42.4 ± 5.54 (10) |
| *mutabilis* | 241.2 ± 12.57 (10) | 272.7 ± 19.62 (10) | 53.4 ± 3.31 (33) | 17.7 ± 1.06 (28) | 44.9 ± 4.47 (27) |
| *vumbae* | 251 ( 1) | | 57 ( 1) | | 49 ( 1) |
| *chirindensis* | 229.9 ± 8.76 (12) | 281.5 ± 15.94 (13) | 56.1 ± 3.34 (14) | 19.0 ± 2.35 (14) | 47.0 ± 6.75 ( 6) |
| *beirae* | 211.8 ± 21.57 (17) | 254.2 ± 30.49 (17) | 53.4 ± 2.43 (17) | 17.6 ± 1.00 (13) | 45.8 ± 5.67 ( 6) |
| *H. undulatus* | 233.0 ± 20.67 (18) | 281.0 ± 28.09 (18) | 56.2 ± 3.21 (17) | 17.1 ± 2.11 (16) | 40.1 ± 4.13 (25) |

geographic variation itself. Attention is drawn to main foci of geographic variation but so many localities are represented by single or faded specimens that trends cannot be assessed in detail. It seems most probable that much variation is clinal, and that if more fresh specimens from more localities become available it might be better to reduce the number of subspecies, paralleling Musser's (1968) elegant treatment of *Sciurus aureogaster*. I do not wish to anticipate such a move, however, when adequate evidence is not yet available.

Compared with skins, relatively few skulls were available for study, so it has been necessary to lump data from widely separated localities. This process does not however lead to increased sample variance, so measurements from different geographical populations may approximate to single statistical populations. The montane forms *vumbae* and *chirindensis* are the largest in skull length, and *shirensis* is the smallest (Table 1). None of the differences between the subspecies recognised from skull characters are above the conventional level of subspecific difference (Mayr, Linsley & Usinger 1953: 178).

Body measurements taken in the field are also few and intrinsically unreliable, because they have been recorded in a number of different ways and by a diversity of collectors. It is difficult to know whether they represent real regional differences, or artefacts, but they seem to be poorly related to skull length and often have exceptionally high variance (Table 2).

### *Heliosciurus mutabilis shirensis*

*Macroxus shirensis* Gray, 1867, Ann. Mag. nat. Hist. (3) 20: 327.
*Heliosciurus gambianus smithersi* Lundholm, 1955, Ann. Transvaal Mus. 22: 294.

Description: Paler specimens have the body hairs banded black and whitish, subbasal light band faintly greyer; limbs whitish due to intense speckling; tail hairs banded black and whitish with all light bands of same colour and terminal ones prominent (rather short in Chowo skin); up to 16 light tail rings (very vague in Chowo skin); venter appears pure white, though hairs do have grey bases. Darker specimens have the hairs banded blackish and buffy white to buff, with subbasal light bands buff; speckling on limbs not so intense; tail hairs banded uniformly whitish; tail rings quite discrete; venter whitish to buffy white. A fresh skin from Mtirize R. approaches the Tambarara series (*chirindensis*) but the hair bases are not deep orange buff and do not differ in colour from the terminal light bands; another fresh skin, from Domira Bay, falls between the two Mtirize River skins in general tone.

Material and localities: Pale forms (*'smithersi'*): Zambia: Chowo Mt (1), Fort Jameson (3), Marble Hill Camp, Lusaka Dist. at 15° 40' S, 28° 37' E (2) — BM; Mafinga

Mtns — Ansell & Ansell, 1973. Zimbabwe: Lundi-Sabi confluence (type locality of *smithersi*) — Lundholm, 1955. Mozambique: Musapa Gap, N end of Chimanimani Mtns; Haroni-Lusitu confluence — Smithers & Tello, 1976. Darker forms and referred specimens: Malawi: Domira Bay (1), NW Nyasa (1), S Angoniland (1), Shire River (type locality of *shirensis,* 3 cotypes) — BM; Chinteche; Ncheu — Ansell, Benson & Mitchel, 1962. Zambia:Mtirize R (2), Nyika Plateau (1), Petauke (3) — BM; Lusito confluence, Gwembe Dist. — Ansell, 1960; Chilongozi Game Reserve; Kalichero; Luano Valley; 4 mi NW of Lundazi; Lusingazi confluence; Mpomwa Hills; Rufunsa rest house — Ansell, 1964; Makutu Mtns; island in L. Kariba, at 1627-D-4; and recorded from 17 quarter-degree squares — Ansell, 1978. Tanzania: Rungwe (2) — AMNH; Igale, Poroto Mtns; Madehani, Ukinga Mtns; Nkuku forest, Rungwe Mtns — Allen & Loveridge, 1933; 4 localities mapped by Kingdon (1974: 428), as *mutabilis,* in part. Long-furred form: Malawi: Komba forest, Misuku Mtns (2) — BM.

### *Heliosciurus mutabilis beirae*

*Heliosciurus mutabilis beirae* Roberts, 1913, Ann. Transvaal Mus. 4: 78.

Description: Body hairs banded blackish and whitish to buffy white; subbasal bands to body hairs rich buff orange; faint orange buff wash on median light bands of tail hairs; light tail rings discrete; venter whitish.

Material and localities: Tanzania: Hokororo, Liwale (1); Masasi (1); Nachinwea (2); Mt Mwemkuru Juu, Liwale (1); Songea (1) — BM; Rondo, Lindi (1) — FMNH; Lindi (1); Mikindani (1) — ZMB; 10 localities mapped by Kingdon 1974: 428, as *H. rufobrachium mutabilis* in part. Mozambique: Beira, type locality of *beirae,* and including Masembeli 23 mi to the NW (12) — BM; Mesito, Tete dist. (1); Chimonzo (1; most southerly record of genus, not mapped by Smithers & Tello, 1976) — USNM.

### *Heliosciurus mutabilis chirindensis*

*Heliosciurus mutabilis chirindensis* Roberts, 1913, Ann. Transvaal Mus. 4: 78.

Description: Body hairs banded dark blackish brown and ochre (darker than in other skins), with subbasal light bands deep buff orange (3 Selinda skins and 3/5 of the fresh Tambarara skins); tail hairs banded buffy white, with ochre wash to median band in Selinda and 1 Tambarara skin; tail rings well marked; venter variable, buffy white with ochre marginal wash (3 Tambarara, 2 Selinda), deep ochre (2 Tambarara, 2 Selinda) or grey brown, much as flanks but paler (2 Tambarara, one with deep ochre to underside of limbs).

Material and localities: Zimbabwe: Chirinda forest, type locality of *chirindensis* (3) — BM; Mt Selinda (1) — CM; East Highlands Tea Estate, foot of Inyangani Mt, Inyangani dist. (1) — USNM; Ngorima Tribal Reserve (Tribal Trust Land) East, Melsetter dist., Manicaland (1) — USNM. Mozambique: Tambarara (7) — BM; Lusitu (1) — USNM.

### *Heliosciurus mutabilis mutabilis*

*Sciurus mutabilis* Peters, 1852, Reise nach Mossambique. Säugethiere, p. 131.

Description: Body hairs dark shining brown, almost black, in very fresh specimens, speckled with bright yellowish buff, approaching Selinda skins (Mlanje, Chiradzulu), soon fading to dark maroon-brown, speckled to between buff and cold buffy white; subbasal bands to hairs buff to buffy-grey, but warm buff to dull orange ochre in a few specimens, again approaching *chirindensis;* light bands to tail hairs usually buffy white, with a tinge of orange in the median band in a few specimens; light tail rings not very well demarcated; venter whitish grey or yellowish grey, to brown grey, in a very few specimens almost as dark as flanks. In 19/42 skins (excluding 6 juveniles), a broad dark dorsal stripe is present, beginning at forehead, on mid back or somewhere between, and extending to tail, in which the hairs are unicolourous, lacking the light bands. In some specimens, the dorsal stripe broadens onto the flanks and rump, but muzzle and legs always retain the speckling. The tail hairs in these more intensely pigmented specimens retain the light bands, or at least the more distal ones, which become relatively narrow; rarely they may lose them altogether (two specimens, Mlanje and Chiradzulu). Squirrels with a dark dorsal band are recorded from all the localities listed below except Soche and Liwondo (singletons only from each of these places).

Material and localities: Malawi: Chiradzulu (6), Chiromo (3), Cholo Mt (1 & 2 AMNH), Likungala R (9 & 1 AMNH, 1 USNM), Liwondi (1), Luchinga R (1), Mlanje Mt (5 & 1 AMNH), Namuli Mt (1), Soche Mt (1), Zomba (20) — BM; Mozambique: Masindi Mt (1) — BM; Boror (type locality of *mutabilis)* — Peters, 1852.

### *Heliosciurus mutabilis vumbae*

*Heliosciurus mutabilis vumbae* Roberts, 1937, Ann. Transvaal Mus. 19: 100.

Description: Resembles the most intensely pigmented specimens of nominate *mutabilis,* but with the belly concolourous with the flanks, and with the dark dorsal band not as well developed at least in the specimens seen.

Material and localities: Zimbabwe: Vumba, type locality of *vumbae* (2) — TV; Manchester Gardens (Vumba Botanical Reserve), Vumba National Park (1) — USNM; Cecil Kop, Umtali (1) — CM; Stapleford — Smithers & Wilson, 1979. Mozambique: Macequece (1) — TV.

### *Heliosciurus undulatus*

*Sciurus undulatus* True, 1892, Proc. U. S. nat. Mus. 15: 465.
*Heliosciurus undulatus dolosus* Thomas, 1909, Ann. Mag. nat. Hist. (8) 4: 100.

*Heliosciurus undulatus daucinus* Thomas, 1909, Ann. Mag. nat. Hist. (8) 4: 101.
*Heliosciurus undulatus marwitzi* F. Müller, 1911, Zool. Anzeiger 37: 76.
*Heliosciurus rufobrachiatus shindi* Heller, 1914, Smithsonian misc. Coll. 63 (3): 7.

Differs from *H. mutabilis* in being on average slightly smaller (95 percent of occipito-nasal skull length measurements 51.2.–56.7 mm against 52.5–57.8 mm; body measurements not significantly different); in having 9 or more bands on the tail hairs, as against 7–8 in most lowland *H. mutabilis* populations, even though the tail hairs are shorter than in the latter (Table 3); and in not bleaching between moults. The feet and hands are usually but not always suffused with orange. These differences are not great, but they are distinct and until we are more certain of species limits in the genus, it seems best to retain *undulatus* as a separate species.

Table 3. Frequency distributions of numbers of agouti-bands on tail hairs of *Heliosciurus* species

| | Number of bands | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| *H. mutabilis* ssp. *shirensis* and *mutabilis* | | 3 | 17 | 9 | 2 | | | |
| Komba forest *(shirensis)* | | | | | | | | 2 |
| ssp. *beirae* | | | 5 | 8 | 3 | 1 | | |
| ssp. *chirindensis* | | | | | 5 | | | |
| *H. undulatus* | | | 1 | 2 | 14 | 5 | 4 | |

Subjectively, variation in *H. undulatus* in colour is less extensive than in *H. mutabilis*. Individual squirrels are never as dark as *H. m. mutabilis* or *vumbae*, nor as pale as the lightest *H. m. shirensis*. Within population variation can be considerable, as Allen & Loveridge (1942) discovered in 15 specimens from Magrotto Mtn, Tanzania. There is also a degree of geographic, probably clinal, variation. Specimens from higher altitudes, corresponding to the type, are darker and more richly coloured; those from the north of the species range (*shindi, daucinus*) are paler; and those from the south, including Zanzibar and Mafia (*dolosus*) are duller and greyer. The populations on Mafia and Zanzibar are involved in the clinal trend and should not be regarded as an insular subspecies even if a southern subspecies is recognisable. However, specimens from intermediate localities are difficult to assign to a

particular nominal subspecies, as Allen & Loveridge found with specimens from Tanga, and if the described forms were to be considered valid, then additional subspecies would have to be named — for example, a BM specimen from Tamota, Mandeni is exceptionally dark below, the hairs blackish with an orange band.

Description: Body hairs banded blackish with a whitish subterminal band and usually three contrasting dull orange ochre to deep orange more proximal bands; tail hairs similarly banded; 10–14 black tail rings; venter whitish grey to ochre, darker on limbs, or deep dull ochre, sometimes with vague paler median band; face, nose and feet suffused with pale grey ochre to orange ochre.

Material and localities: Tanzania: Amani (2), Dar es Salaam (1), Mafia I., type locality of *dolosus,* including Kilindoni (4), Mshindasi R, Kidodi, Kilosa (1), Mweka (2), Usambara Mtns (1), Tamota, Mandeni, N. Prov. (1 & 1 AMNH), Zanzibar, including Mkunduchi and Jambiani (4) — BM; Kahe (1) — USNM; Nguru Mtns (2) — CM; Bungu, Usambara (1) — FM; Kibongoto (1), Kilimanjaro (1), Kindi, Pangani (1) — ZMB; Mt Kilimanjaro, type locality of *undulatus* — True, 1892 — and of *marwitzi* — Müller, 1911; Mombo, Usambara; Kibongoto, Kilimanjaro, 2,000 ft — Lonnberg, 1910; Pangani; Tanga — Müller, 1911; Siga Caves near Tanga; Magrotto Mtns — Allen & Loveridge 1942; Arusha; Bumbali; Mkulumuzi Caves — Swynnerton & Hayman, 1951. 13 localities plotted by Kingdon (1974: 428). Kenya: Kwali forest, Shimba Hills (4), Marima Hills (1), Mombassa (1, type of *daucinus*), Digo Dist., Msambweri/Ramisi (3), Witu (1) — BM; Mazeras (1) — USNM; Kilifi Dist., 1 mi SW Gedi (2) — AMNH; Pokomoni, Tana (1) — ZMB; Mt Umengo, Taita Hills, type locality of *shindi* — Heller 1914; Mt Mbololo — Allen & Lawrence, 1936. 8 localities plotted by Kingdon (1974: 428).

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## Summary

The sun squirrels *Heliosciurus mutabilis* and *H. undulatus* are considered to be specifically distinct from *H. gambianus* and *H. rufobrachium*. *H. undulatus* is regarded as monotypic, while *H. mutabilis* is provisionally treated as a polytypic species with five subspecies.

## Zusammenfassung

Die Sonnenhörnchen *Heliosciurus mutabilis* und *H. undulatus* werden als artlich verschieden von *H. gambianus* und *H. rufobrachium* angesehen. Dabei wird *H. undulatus* als monotypisch angesehen, während *H. mutabilis* vorläufig als polytypische Art mit fünf Unterarten behandelt wird.

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